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Ecological niche of three teuthophageous odontocetes in the northwestern Mediterranean Sea

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Abstract

In the northwestern Mediterranean Sea, sperm whales, pilot whales and Risso's dolphins prey on cephalopods exclusively or preferentially. In order to evaluate their competition, we modelled their habitat suitability with the Ecological Niche Factor Analysis (ENFA) and compared their ecological niche using a discriminant analysis. We used a long term (1995–2005) small boat data set, with visual and acoustic (sperm whale) detections. Risso's dolphin had the shallowest and the more spatially restricted principal habitat, mainly located on the upper part of the continental slope (640 m mean depth). With a wider principal habitat, at 1750 m depth in average, the sperm whale used a deeper part of the slope as well as close offshore waters. Finally, the pilot whale has the most oceanic habitat (2500 m mean depth) mainly located in the central Ligurian Sea and Provençal basin. Therefore, potential competition for food between these species may be reduced by the differentiation of their ecological niches.

1 Introduction

The ecological niche of a species is a complex set of variables characterized by three principal axes: habitat (influence of environmental factors defining the spatial distribution), diet (prey species, trophic level) and seasonality (use of resources and space according to time) (Frontier and Pichod-Viale, 1998; Lévêque, 2001). Theoretically, each species has its own ecological niche and two species sharing close niches, i.e. same prey species and distribution area, will be in competition. If the first species is more efficient in exploiting these resources, the second one will be excluded partially or totally from the area (Frontier and Pichod-Viale, 1998; Lévêque, 2001). Otherwise, specialization of both species will occur with emergence of different seasonality, and/or with a specialisation or a diversification of the diet (Whitehead et al., 2003).

In the northwestern Mediterranean Sea (NWMS) (Fig. 1a), the sperm whale (*Physeter macrocephalus*), the long-finned pilot whale (*Globicephala melas*), Risso's

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dolphin (*Grampus griseus*) and Cuvier's beaked whale (*Ziphius cavirostris*) are teuthophageous, i.e. they prey on cephalopods exclusively or preferentially (Astruc and Beaubrun, 2005). The three former species have been shown to be common over the whole study area, while the latter displays a more restricted distribution (Azzellino et al., 2003; Gannier, 1999; Podesta et al., 2006). Our surveys covered most of the NWMS (Fig. 1a) and resulted in only three observations of Cuvier's beaked whale. Consequently, our work did not deal with this species.

Stomach contents of stranded animals in the Mediterranean show an overlap of the diet of sperm whales, pilot whales and Risso's dolphins. Their principal preys are few species of bathypelagic cephalopods of the Histioteuthidae and Ommastrephidae families (Astruc and Beaubrun, 2005). Furthermore, previous studies highlighted similar trends in their distribution. The sperm whale, the most studied species, seems to be opportunistic in its feeding strategy, exploiting areas with steep slopes, as well as offshore waters featuring SST fronts (Gannier et al., 2002; Gannier and Praca, 2007). The Risso's dolphin seems to prefer waters with steep slopes from 500 to 2000 m (Bompar, 1997; Gannier, 1998b), while the pilot whale might prefer more oceanic areas, with waters deeper than 1000 m (Gannier, 1998b). But the studies on Risso's dolphins and pilot whales were principally conducted in the Ligurian Sea and/or in the Gulf of Lions and did not cover the entire NWMS.

As a possible competition between these species may occur, it was interesting to improve the knowledge on their ecological niches and in particular on their habitats. The present study focuses on the influence of environmental factors, in the whole basin and for a ten years time scale. We modelled their habitat suitability with the Ecological Niche Factor Analysis and compared their niches with a discriminant analysis.

2 Material and methods

2.1 Study area

The NWMS (between 2.5° E and 9.5° E, 39.5° N and 44.5° N) has complex topographic and oceanographic features (Fig. 1b). Both steep and narrow slopes (Provence, Balearic and north-eastern Corsican coasts) and large smooth continental shelves (Gulf of Lions, western Sardinian coast) are encountered (Biju-Duval and Savoye, 2001). The topography and wind regime lead to a cyclonic circulation of modified Atlantic waters from the Ligurian to the Balearic Sea. The Ligurian front (LF) and the North Balearic front (NBF) are permanent, seasonally fluctuating fronts, whereas the presence of fronts between waters of the North-Mediterranean current (NMC) and cold upwelled waters from the Gulf of Lions depends on the occurrence of Mistral and Tramontane winds (Le Vourch et al., 1992; Lopez-Garcia et al., 1994; Millot, 1999; Millot and Wald, 1990). Although an oligotrophic basin, generally unproductive, the NWMS features an important phytoplankton bloom with chlorophyll concentration peaking between 0.8 and 2.5 $mg\,m^{-3}$, generally occurring in March (Morel and André, 1991). In the Gulf of Lions, the Rhône river brings high quantity of nutrients and particles (Conan et al., 1998), increasing the turbidity. This phenomenon leads to an overestimation of chlorophyll concentrations in satellite data (>0.8 $mg\,m^{-3}$ even in summer) and the Rhône panache can be classified as turbid case 2 water (Antoine et al., 1996). Consequently, the area influenced by the panache of the Rhône was removed from our analysis.

2.2 Data collection and standardisation

Dedicated surveys were conducted on a motor-sailing boat in summer from 1995 to 2005. The protocol combined visual searching and systematic discrete acoustic sampling (for details see Gannier, 1998a; Gannier et al., 2002). In brief, the visual searching was conducted by three observers scanning continuously with naked eyes from

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abeam forward on both sides of the vessel. The acoustical sampling used a towed hydrophone and consisted of listening for 1 min every 2 nm (3.7 km) along the cruise track. Sperm whales were recognized by their typical signal composed of regular clicks (Teloni, 2005). For pilot whales and Risso's dolphins, only visual detections were used, because their acoustic signals could be confused mutually and with other delphinids. At each listening or visual sighting, sea state, position of the boat and of the animals, visual conditions (V, varying between 0 and 6), background acoustic noise (U, varying between 1 and 5) and the bio-acoustic signal levels (SL, varying between 0 and 5) were recorded. V, U and SL were subjectively estimated by experienced observers. Data with V<4, U>3 or SL<2 were removed from the data set.

In order to avoid autocorrelation in the analysis, data were merged into observation sequences in ArcGIS 8.3©. For sperm whales, all acoustical or visual successive observations obtained without a minimum of one hour time-lag were considered as from the same animal or group (Gordon et al., 2000). For positioning the observation sequence, we chose either the location of a visual sighting or of the acoustic detection with the best SL. For pilot whales and Risso's dolphins, the location of the first visual sighting was chosen.

The Eco-Geographical Variables (EGVs) were classical data used in cetacean habitat modelling (e.g. Cañadas et al., 2002; Hamazaki, 2002), related to topography, temperature, salinity and primary production. Depth was obtained from the GEBCO© Digital Atlas (IOC – IHO – BODC, 2003). It was used to calculate the slope and the distance to the 200 m contour, which was shown to be more relevant than coast contour for those species (Mangion and Gannier, 2002). Sea Surface Temperature (SST) data were downloaded, depending on their availability, from the websites of the Pathfinder sensor for 1995 to 2002 data (PO.DAAC) and of the Modis sensor for 2002 to 2005 data (OceanColor). The front detection maps were computed on the basis of SST maps, using a Sobel filter available in Idrisi Andes©, which was more efficient than a standard deviation in highlighting temperature gradients. Salinity data from 1889 to

2002 were obtained from the MEDAR / MEDATLAS II database (MODB) and chlorophyll concentrations data for the 1998 to 2005 period from the SeaWifs sensor website (OceanColor).

For the hydrological and biological EGVs, we used monthly maps to compute average situations for two periods: the summer (sum: June, July and August) and the phytoplankton bloom period (phy: February, March and April). These seasonal maps were then averaged over all years of the survey period, resulting in two seasonal maps for each EGVs. Salinity and chlorophyll concentration were not available for all years, but available data overlapped 80% of the survey period and were considered to be representative of average conditions.

A 9×9 km grid cell of the study area was created with Idrisi Andes©, in which both species and environmental data were implemented. This resolution was chosen in order to use chlorophyll concentration data that were not available at higher resolution for monthly maps.

2.3 Habitat modelling

Classical habitat modelling techniques (e.g. Generalised Linear Model – GLM or Generalised Additive Model – GAM) are based on presence-absence data (Guisan and Zimmermann, 2001; Redfern et al., 2006). "True" absence data (when animals are actually absent) are not easy to collect for mobile or inconspicuous species, such as cetaceans which are able to spend long periods underwater. Biases may be caused by 'false' absence data, when animals are present but not detected. For pilot whales and Risso's dolphins, such biases could not be avoided by the use of acoustic data collected along the survey track, as for sperm whales. Then we choose to use a presence-only method: the Ecological-Niche Factor Analysis (ENFA) (Hirzel et al., 2002).

Detailed description of the ENFA and its mathematical computations are given in Hirzel et al. (2002, 2006b). The ENFA is a presence-only multifactorial analysis, comparing the distribution of the species to the global available environment in the hyper-

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space define by the EGVs. The transformation of EGVs in a set of uncorrelated factorial axes introduces ecological significance. Marginality (how much a species' habitat differs from the mean available conditions) is represented in the first factorial axis, and specialisation (breadth of the ecological niche) is maximised in the subsequent axes. The factorial axes coefficients are used to compute global marginality (M, varying generally between 0 and 1) and specialization (S, indicating some degree of specialization when superior to 1). Finally, a Habitat Suitability (HS) map is built with the median algorithm, which compares the position of each cell of the study area to the distribution of presence cells on the different factorial axes. A cell adjacent to the median of an axis would score 100 and a cell outside of the species distribution would score zero. All the ENFA analyses were conducted using Biomapper 3.2© software (Hirzel et al., 2006a).

2.4 Model validation

The model validation was realised with a k-fold cross-validation, evaluated by a "continuous Boyce index" B (Boyce et al., 2002; Fielding and Bell, 1997; Hirzel et al., 2006b). The presence data set is partitioned in k independent subsets, and k-1 partitions are used in the calibration data set, leaving the last partition as the validation data set. The number of partitions k was chosen following the Huberty's rule for the pilot whale (k=4) and Risso's dolphin (k=3) (Fielding and Bell, 1997). For the sperm whale, k was fixed to 10, which seems to be the best number of partitions when there are more than 100 cells with observed presence (Hirzel et al., 2006a).

The predicted-to-expected ratio F_i is calculated as:

$$F_i = \frac{P_i}{E_i} \quad (1)$$

$$P_i = \frac{O_i}{\sum O_i} \quad (2)$$

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$$E_i = \frac{A_i}{\sum A_i} \quad (3)$$

In Eqs. (1), (2) and (3), P_i is the predicted frequency of evaluation cells, with O_i the number of validation cells falling in an HS window i and $\sum O_i$ the total number of validation cells. E_i is the expected frequency of evaluation cells, with A_i the number of cells belonging to the same HS window i and $\sum A_i$ the total number of cells in the whole study area.

F_i is first computed in the HS window [0;20], then the window is shifted upward from one HS unit and F_i is computed again. This operation is repeated until the moving window reaches the last possible range [80;100] and provides a predicted-to-expected ratio curve (p/e curve). For a random model, F_i=1 for every window i. If a model properly predicted the suitable areas of one species , F_i<1 in windows with low HS index values and F_i>1 for windows with high HS index values, and it features a monotonically increasing p/e curve. It is evaluated with B, which is a Spearman rank correlation between F_i and the average HS index of the different windows (Boyce et al., 2002). B varies between −1 and 1. The p/e curves and B are produced k times, each time leaving out another validation partition, allowing the assessment of their central trend and variance (here we present the mean ±SD). The threshold between predicted absence and presence cells was estimated using the p/e curve, following Hirzel et al. (2006b).

2.5 Niche differentiation

In addition to the habitat suitability models, a discriminant analysis was realised to compare the ecological niches of the sperm whale, the pilot whale and Risso's dolphin (Legendre and Legendre, 1998). This technique is a multivariate analysis using the space defined by the EGVs and the species distributions simultaneously. It computes discriminant factors that maximise the interspecific variance and minimize the intraspecific variance. The discriminant factors are used, in Biomapper 3.2©, to compute indexes quantifying the niches breadth and overlap. The Hurlbert index (B') measures

the breadth of the niches. It varies between 0 (corresponding to species ultimately specialised) and 1 (corresponding to generalist species) (Hurlbert, 1978). The Lloyd's asymmetric overlap index (Z) evaluates the overlapping of species niches two by two. $Z_{x(y)}$ is the part of the niche of X, which is also shared by Y. In other words, it is the overlapping of the niche of Y on the niche of X (Hurlbert, 1978).

3 Results

3.1 Habitat suitability models

All global marginality, specialisation and Boyce indices are presented in Table 1. Boyce indices decreased with the number of presence cells from 0.61 for the sperm whale to 0.39 for the Risso's dolphin. All three species displayed a high marginality, 0.77 to 1.11, but specialisation coefficients were more variable (from 1.40 to 3.31).

3.1.1 Sperm whale

The total number of presence cells was 175 for the sperm whale. The model of this species had a B=0.61±0.50 and a quasi-monotonic p/e curve which indicates a highly fitted model (Hirzel et al., 2006b). From these curves, the habitat suitability threshold between predicted absence and presence was estimated to 56 (Fig. 2a). This species had an overall marginality of 0.77 and an overall specialisation of 1.40, indicating that its ecological niche is different from the mean habitat available, but still quite wide.

The marginality factorial axis indicated a strong relationship for cells with steep slope (coefficients of 0.49) and close to the 200 m contour (−0.42). This axis also showed importance of high chlorophyll concentrations in summer (0.42) and low SST for summer (−0.38) and for phytoplankton bloom period (−0.31). Specialisation axes highlighted the restriction of the species to the lower SST (coefficients varying between 0.61 and 0.71 in spring), lower salinity (0.32 for the summer and 0.37 for the phytoplankton

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bloom period) and higher chlorophyll concentrations (0.72 in summer). Bottom depth did not seem to be an important variable for this species (Table 2). The consequent HS map showed a core habitat on the continental slope of the whole area, including the Balearic and Corsica islands, and in close offshore waters (Fig. 3a).

3.1.2 Pilot whale

The total number of presence cells for the pilot whale was 33. This model had a B of 0.58±0.19 meaning a well fitted model. Its p/e curve increased quasi-monotonically between 39 and 90 HS index, but decreased between 0 and 39, and between 90 and 100. For this species, the threshold between predicted absence and presence was estimated to 49 (Fig. 2b). The strong global marginality of 0.85 and the high total specialisation of 3.31 indicated that pilot whales have a restricted ecological niche in comparison with the mean environment of the study area.

Both marginality and specialisation axes highlighted a strong relationships with the colder SST for summer (marginality of −0.57 and specialisation of 0.42) and phytoplankton bloom period (−0.49 for the marginality, 0.42 and 0.82 for the specialisation), and higher chlorophyll concentrations in summer (marginality of 0.51 and specialisation of 0.77). The first specialisation axis also showed a restriction to deep waters (coefficient of 0.37) (Table 3). The HS map highlighted a principal habitat in oceanic waters of the central Ligurian Sea and Provençal basin (Fig. 3b).

3.1.3 Risso's dolphin

The total number of presence cells was 23 for Risso's dolphin. The ENFA typically requires a number of EGVs less than 1/2 to 1/3 of the number of presence cells (A. Hirzel, personal communication). The number of possible EGVs was then limited for this species and we constructed a model keeping only some of them. We carried out a step-by-step descending exclusion of the EGVs and choose the model with the best validation.

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The model for Risso's dolphin was less meaningful than for the two other species, with a B=0.39±0.21 and a more variable p/e curve. The threshold between predicted absence and presence was estimated to 49 (Fig. 2c).

The marginality axis indicated a strong relationship with steep slope (coefficient of 0.64), low distance to the 200 m contour (−0.63) and a certain affinity for shallow areas (depth coefficient of −0.30). The affinity for cells close to the 200 m contour was important in each specialisation axes (coefficients from 0.43 to 0.61). These axes also indicated an affinity for higher chlorophyll concentrations in summer (0.77) and steeper slopes (0.73) (Table 4).

In relation to a very high marginality >1 and important specialisation (1.89), the principal habitat for Risso's dolphin was very limited. It was located on the upper part of the continental slope of the whole study area (Fig. 3c).

3.2 Niche differentiation between the three species

For the discriminant analysis, we limited the number of EGVs, to those highlighted as important by the ENFA. The first and second discriminant factors had eigenvalues of 36.53 and 12.49 respectively, meaning that they well discriminated the specific niches. As the two discriminant factors highlighted the same trends and as the eigenvalue of the first factor was three time higher than that of the second, we only used the first. The distribution ranges of species observations along the axis showed that niches of Risso's dolphins and pilot whales were well separated, while the niche of sperm whales was more extended and overlapped the two previous (Fig. 4). EGVs with positives values seemed in favour of Risso's dolphin and showed a more coastal habitat, with the influence of an important slope, relatively warm waters with high chlorophyll concentrations and low distance to the 200 m contour (Table 5). On the contrary, the observations of pilot whales were linked to EGVs with negative values and highlighted an offshore habitat with important depth and relatively high salinity (Table 5). The distribution of sperm whale observations had a principal peak in the negative values, but there were important number of observations in positive values too: the discriminant analysis was

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not able to highlight a particular trend of this species habitat.

The Hurlbert's niche breath index indicates that the sperm whale had the wider niche (B'=0.62), followed by the pilot whale (B'=0.55) and Risso's dolphin that seemed very specialized for its habitat (B'=0.02). The Lloyd's asymmetric overlap indexes (Table 6) confirmed that the niche of the sperm whale overlapped an important part of both niches of the pilot whale and Risso's dolphin (respectively Z=18.45 and 3.00), while the reciprocal overlaps were small (Z=3.47 for the pilot whale and Z=0.37 for Risso's dolphin). Furthermore, the niche overlap indexes of pilot whales and Risso's dolphin were nil, meaning their niches were totally separated.

4 Discussion and conclusion

4.1 Model evaluation

ENFA produced meaningful habitat predictions for three species with variable amounts of presence data: using 175 cells of presence for the sperm whale and 33 for the pilot whale, we obtained well fitted models. For Risso's dolphin, the validation was less satisfactory, certainly as a consequence of limited number of presence cells of this species. Nevertheless, the HS maps produced for this species are in general agreement with studies on its distribution (Azzelino et al., 2001; Gannier, 1998b). While GLM or GAM seem to be more accurate than ENFA (e.g. Brotons et al., 2004), this later is a useful tool when absence data are not available, or when species are rare.

The use of data compiled and averaged on a long-term scale, for 3 months seasonal periods, introduced some fading for oceanographic features at small scale, such as moving SST fronts or rich water masses. The impact of such temporal averages on our model is difficult to evaluate and no study, to our knowledge, compared the evolution of the distribution of teuthophageous odontocetes at a monthly scale. The spatial pooling of presence data in the NWMS clearly attenuated the accuracy of our models at smaller scale. For example, taking account of observations in the Ligurian Sea alone,

the sperm whale could have a deeper habitat than the one we modelled (Gannier, 1998b). Similarly, away from topographic features, thermal fronts, and in particular the NBF, seem to be favourable to sperm whales (Gannier and Praca, 2007). The offshore presence cells (at least 20 km from the 2000 m contour for these authors) correspond to only 19% of our data set. For this reason, they were not considered as representative of the main habitat in the modelling process. Nevertheless, our modelling strategy was to attempt a global description in a temporally and spatially heterogeneous area, the entire NWMS, instead of modelling habitat in restricted and more homogeneous regions, as proposed by Cañadas et al. (2002) for odontocetes or Panigada et al. (2005) for fin whales (*Balaenoptera physalus*).

4.2 Comparison of the ecological niches

The summer habitat niches of pilot whale, Risso's dolphins and sperm whales seemed to be segregated and differ in their habitat component. The pilot whale presented the most oceanic habitat with a strong relationship with lowest SST, important chlorophyll concentrations and depth. Risso's dolphin has the shallowest habitat, on the upper part of the slope, and is mainly influenced by the proximity of the 200 m contour. The sperm whale has the wider habitat, on the whole continental slope, and slightly offshore, and seems to be influenced by both topographical and hydrological factors. This is confirmed by the mean depths of the predicted presence areas (i.e. cells with HS values superior to the threshold between absence and presence, Fig. 2), respectively 638 m for Risso's dolphin, 1746 m for the sperm whale and 2511 m for the pilot whale. The mean slope (3.35° for Risso's dolphin, 2.08° for the sperm whale and 0.55° for the pilot whale) and the mean summer SST (respectively 22.19, 21.91 and 21.72°C) followed the same trend.

In the Alboran Sea, southwestern Mediterranean, the three species seem to have closer habitats. Risso's dolphin and the long-finned pilot whale are found in waters deeper than 600 m and the sperm whale in waters deeper than 700 m (Cañadas et al., 2005; Cañadas et al., 2002). Regarding the slope, the species most influenced by

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this factor seems to be Risso's dolphin which preferred slopes higher than 40 m km^{-1} (2.29°), followed by the pilot whale (between 20 and 80 m km^{-1}, i.e. 1.15 and 4.58°) and the sperm whale which did not show any preference (Cañadas et al., 2002). In the Gulf of Mexico, a tropical area, the preferred depths of the sperm whale, Risso's dolphin and the short-finned pilot whale (*Globicephala macrorhynchus*) are close to those found in the Alboran Sea (Baumgartner et al., 2001; Davis et al., 1998). Risso's dolphin seems to have similar habitats in the Alboran Sea, Gulf of Mexico and NWMS. For the sperm whale, differences appear for the slope, which seems to have a more important influence in our study area, perhaps due to a steeper slope at the same depth in NWMS (Biju-Duval and Savoye, 2001). In the Alboran Sea and Gulf of Mexico, the pilot whale clearly has a shallower habitat in waters with a steeper slope than in our case.

Pilot whales are reported to be influenced by cold SST (Hamazaki, 2002), the presence of eddies (Davis et al., 2002) or shallow thermocline (Ballance et al., 1997; Davis et al., 1998). In the North Atlantic, genetic analysis on different populations of long-finned pilot whales do not support a simple segregation by distance, but suggest that population isolation occurs between areas of the ocean which differ in SST (Fullard et al., 2000). Similarly in Pacific, populations of the short-finned pilot whale show genetic, morphometric and life history differences related to SST (Kasuya et al., 1988; Wada, 1988). Hence, the pilot whale could be influenced by temperature features more than topographic ones. In the Alboran sea, areas with depth between 1000 m and 2000 m are very reduced and major oceanographic features occur in a shallower area compared to the Ligurian and Provençal basins (Millot, 1999). Furthermore, cold water masses are observed offshore in the NWMS, in relation to the general circulation and in particular to the LF and NBF that conduct to the upwelling of cold deep waters (Millot, 1999; Sournia et al., 1990). In our study area, this influence of temperature features and cold SST on pilot whales could result in an oceanic habitat, more distinct from Risso's dolphins and sperm whales habitats.

Stomach contents of stranded animals were compiled by Astruc and Beaubrun

(2005) for the whole Mediterranean sea. These authors used the Index of Relative Importance (*IRI*) to compare the importance of preyed species in the diet of Mediterranean cetaceans (Cortès, 1997). The sperm whale presents an *IRI* > 90% for *Histioteuthis bonnellii*. The diet of the pilot whale has an IRI between 40 and 50% for *Todarodes sagittatus*, between 10 and 20% for *H. Bonnellii* and *H. reversa*, and the remaining 10% consists of several other species, including some *Gadidae*. Finally Risso's dolphin has the most diversified diet composed of *H. reversa* (*IRI*>30%), *H. bonnellii* and *T. sagittatus* (10<*IRI*<30%) and of several other species with an *IRI*<10%. All together *H. bonnellii*, *H. reversa* and *T. sagittatus* may represent 60 to 100% of the diet of the three predators studied here. These species of cephalopods principally occur at the same depths, between 200 and 800 m (Quetglas et al., 2000), but their spatial distribution in the whole study area is unknown. It is difficult to compare precisely the habitat of the teuthophageous odontocetes and the distribution of their different preys. However, the habitats that we modelled are influenced by topographic and hydrological features, also favourable to cephalopods (e.g. O'Dor and Coelho, 1993; Quetglas et al., 2000).

From our summer habitat results and published stomach contents, three kinds of ecological niches appear. First, Risso's dolphin is very specialized for its habitat, mainly located on the upper part of the continental slope, but seems generalist for its diet. Second, the pilot whale has a quite wide offshore habitat and a relatively generalist diet. Finally, the sperm whale has a wide habitat, on the offshore part of the continental slope, but is very specialized in its diet. The differentiation of ecological niches of the sperm whale, the pilot whale and Risso's dolphin could then tend to reduce their competition for food resources. However, stomach content of stranded animals may lead to biases (Santos et al., 2001), further investigations on their diet with recent techniques such as stable isotopes or fatty acid analyses will provide more precise information on this part of their ecological niche.

The temporal evolution remains the less known part of the ecological niche of the teuthophageous odontocetes. At a daily scale, the use of passive acoustic or tags allows to show that sperm whales seem to be daytime feeders (Drouot et al., 2004;

Watwood et al., 2006), while pilot whales seem to be predominantly night feeders (Baird et al., 2002). The daily feeding pattern of Risso's dolphin is still unclear. The seasonal variation of the habitat of the three species is difficult to assess in a large area like the NWMS and would require considerable observation effort.

4.3 Perspectives

The modelling of the teuthopageous odontocetes habitat showed a partial spatial segregation between sperm whales, pilot whales and Risso's dolphins in the NWMS. These species are exposed to anthropogenic impacts such as ship collision, noise disturbance and occasionally net entanglement. Our habitat modelling could help the International Sanctuary for Marine Mammals to implement efficient protection measures. Furthermore, cetaceans are fragile species at the top of the food web and dependent on a fluctuating environment. Modelling their habitat and understanding the influence of environmental factors will enable us to assess the effect of the global climate change on their distribution and abundance. As it does not need extensive data sets or absence data, ENFA is a useful tool for such objectives.

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Table 1. Continuous Boyce index (B, varying between –1 and 1), global marginality (M, varying generally between 0 and 1) and specialisation (S, indicating some degree of specialization when superior to 1) for the sperm whale, the pilot whale and the Risso's dolphin.

Species	B (mean ±SD)	M	S
sperm whale	0.61±0.50	0.77	1.40
pilot whale	0.58±0.19	0.85	3.31
Risso's dolphin	0.39±0.21	1.03	1.89

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Table 2. Relevant axes (with their eigenvalues) and the EGV coefficients of the sperm whale model. The positive or negative sign is relevant for the first axis coefficients, but in the following axes only the absolute value of coefficients is considered.

	Axis 1 (0.18)	Axis 2 (0.20)	Axis 3 (0.13)	Axis 4 (0.11)
Depth	−0.03	0.11	0.05	0.17
C. Chloro sum	0.42	0.17	−0.72	−0.05
C. Chloro phy	−0.02	−0.02	0.11	−0.01
Dist. 200 m	−0.42	0.22	−0.12	0.19
Salinity sum	−0.23	0.32	−0.05	0.12
Salinity phy	−0.29	−0.37	−0.02	−0.24
Slope	0.49	0.11	0.09	0.18
SST Front sum	0.01	−0.01	−0.02	−0.10
SST Front phy	−0.18	−0.06	−0.24	0.13
SST sum	−0.38	−0.39	0.11	0.57
SST phy	−0.31	0.71	−0.61	−0.69

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Table 3. Relevant axes (with their eigenvalues) and the EGV coefficients of the pilot whale model. The positive or negative sign is relevant for the first axis coefficients, but in the following axes only the absolute value of coefficients is considered.

	Axis 1 (0.33)	Axis 2 (0.31)	Axis 3 (0.15)
Depth	0.18	−0.37	−0.03
C. Chloro sum	0.51	0.77	−0.30
C. Chloro phy	0.16	−0.14	−0.03
Dist. 200 m	−0.09	0.06	−0.05
Salinity sum	0.01	−0.06	−0.18
Salinity phy	−0.01	0.14	0.12
Slope	0.22	−0.20	−0.07
SST Front sum	0.01	0.03	0.03
SST Front phy	−0.24	0.04	−0.07
SST sum	−0.57	0.07	0.42
SST phy	−0.49	0.42	−0.82

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Table 4. Relevant axes (with their eigenvalues) and the EGV coefficients of Risso's dolphin model. The positive or negative sign is relevant for the first axis coefficients, but in the following axes only the absolute value of coefficients is considered.

	Axis 1 (0.46)	Axis 2 (0.25)	Axis 3 (0.17)	Axis 4 (0.08)
Depth	−0.30	−0.16	−0.09	−0.44
C. Chloro sum	0.26	0.77	0.29	0.28
Dist. 200 m	−0.63	0.48	−0.61	0.43
Salinity sum	−0.14	−0.01	0.05	−0.45
Slope	0.64	0.18	−0.73	0.15
SST sum	−0.16	0.34	0.08	0.57

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Table 5. Coefficients of the EGVs along the first discriminant factor.

EGVs	Coefficient values
Depth	−0.339
Salinity sum	−0.129
Slope	0.103
Dist. 200 m	0.132
SST sum	0.538
C. Chloro sum	0.742

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Table 6. Lloyd's asymmetrical overlap indexes ($Z_{x(y)}$) between the niches of the sperm whale, the pilot whale and Risso's dolphin.

Y / X	sperm whale	pilot whale	Risso's dolphin
sperm whale	–	3.47	0.38
pilot whale	18.42	–	0.00
Risso's dolphin	3.00	0.00	–

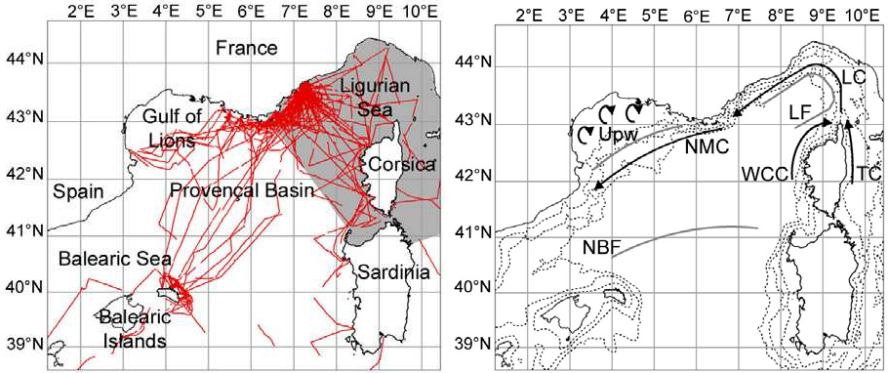

Fig. 1. The northwestern Mediterranean Sea. **(a)** Main basins, the International Sanctuary for Marine Mammals, Pelagos (grey area) and the effort realised during surveys in summer from 1995 to 2005 (red lines); **(b)** Topographic and oceanographic features: 200 m, 1000 m and 2000 m contours (dashed lines), upwellings (Upw), currents (black arrows: WCC – Western Corsican Current, TC – Tyrrhenian Current, LC – Ligurian Current, NMC – North Mediterranean Current) and fronts (grey lines: LF – Ligurian Front, NBF - North Balearic Front).

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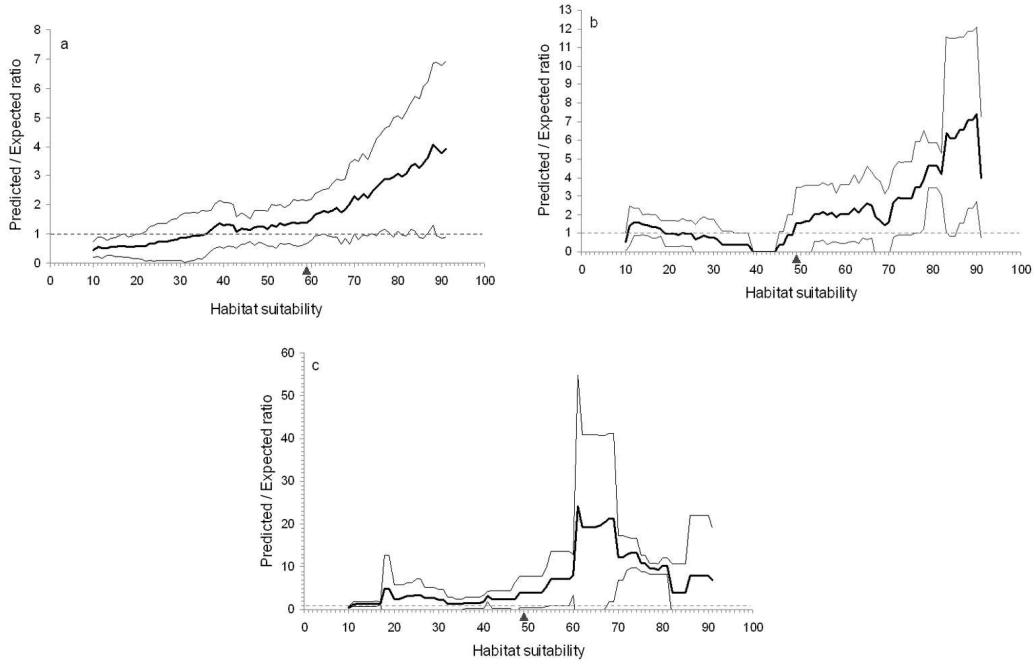

Fig. 2. Predicted-to-expected ratio curve (mean ± SD) and threshold between predicted presence and absence (arrow) for **(a)** sperm whale, **(b)** pilot whale and **(c)** Risso's dolphin models (the limit of random models, predicted-to-expected ratio F_i=1, is indicated by the dotted line).

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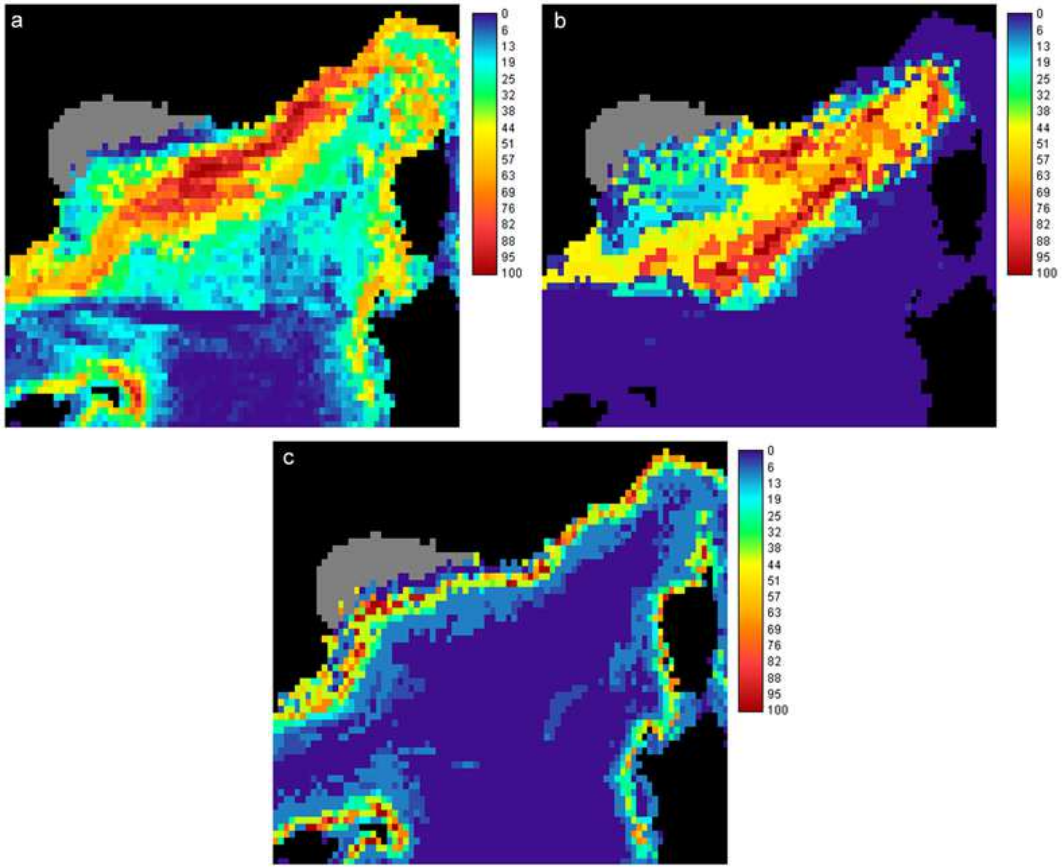

Fig. 3. Habitat suitability maps for **(a)** sperm whale, **(b)** pilot whale and **(c)** Risso's dolphin models (the grey area was removed from the analysis).

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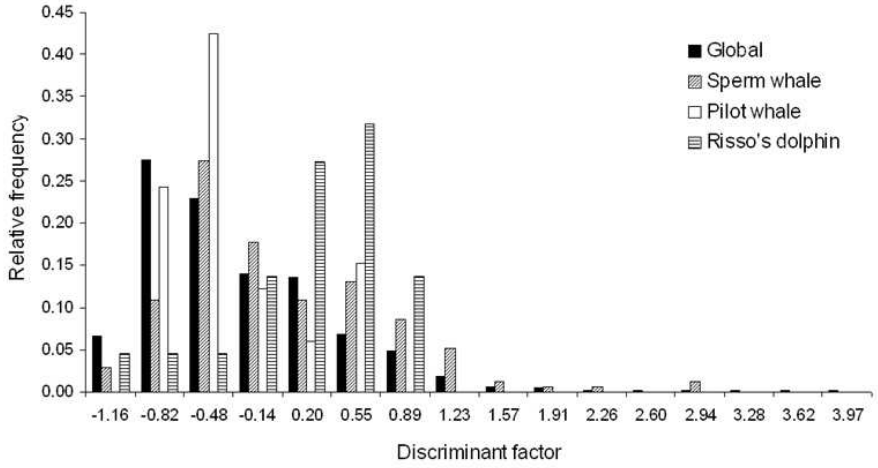

Fig. 4. Distribution of cells of the study area and of observations of the sperm whale, the pilot whale and Risso's dolphin along the first discriminant factor.

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